

Biogeography of the Herpetofauna of the British Virgin Islands, with Description of a New Anole (Sauria: Iguanidae)

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ABSTRACT. Specimens and field data were collected for 44 of 46 named islands in this group. Published lists provide additional data for 24 of the islands visited and both that were not. The islands consistently have more species than areas, elevations, and distances from propagule sources might lead one to predict. There seems to be a basic, minimal number of three species per island, regardless of physical parameters. These are generally an *Anolis*, a member of the family Gekkonidae, and some other reptile. Even tiny rocks and overwashed bars usually support at least an *Anolis*. One such, Carrot Rock, 1.2 ha and 26 m high, supports a remarkable new species of the alpha section of *Anolis*. It is a member of the *crisatellus* group *sensu* Williams attaining very large size, combining two scale characters: 1) dorsals small; 2) digital lamellae count high; and three color characters: 1) chin tricolor; 2) latero-dorsal trunk and neck boldly patterned; 3) a dark bar or blotch on each side of the sacrum. Islands, species, areas, heights, and distances are tabulated and discussed.

INTRODUCTION

The British Virgin Islands constitute the fragmented northeastern extremity of the Greater Antilles. For the most part they are old, folded, and buckled continental strata of grano-diorites, basalt, conglomerates, and slates and shales (Martin-Kaye, 1959). The nether isle of Anegada and some strata scattered on some of the other cays are oceanic limestones deposited during Pleistocene in-

terglacials. These same interglacial seas, standing dozens of meters higher than the sea today, loosened, rolled, and tumbled the rocks in many areas, leaving piles of huge boulders—some as big as a house—signalled today by names like Fallen and Broken Jerusalem.

As sea level fell following the Sangamon Interglacial, some hundred thousand years ago, more and more land was exposed. At the Wurm glacial maximum, the entire Puerto Rico Bank was dry land all the way to Anegada. In the last ten thousand years the rising sea has refragmented the land into fifty or more islands, rocks, and cays. Since the Wurm, sea level has probably never stood higher than it does today; it continues to rise (Morris *et al.*, 1977).

The British Virgin Islands are an artificial entity, separated from their American neighbors by a line passing between Pelican (British) and Flanagan (U.S.) Islands on the south, curving west through The Narrows between the Thatches (British) and St. John (U.S.), and running westward into the North Atlantic south of the Tobagos (British). My study of these islands involved 40 days of field work in March and April, 1980. Not counting rocks with no more than herb-stage vegetation, I tallied 46 islands suitable for reptiles and/or amphibians (see Fig. 1). I visited all of these except Jost Van Dyke and Mosquito, both large islands, often and easily visited, and both with good species lists. It is un-

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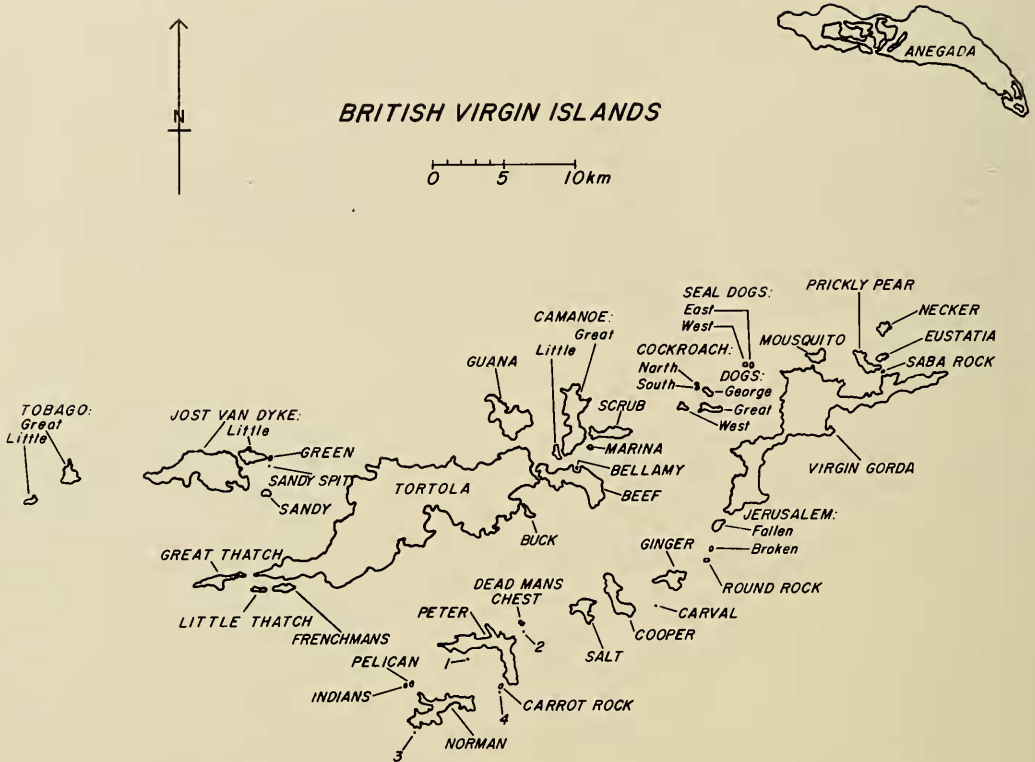


Figure 1. The British Virgin Islands. Four nameless cays are numbered. (Modified from Marler, 1973.)

likely I could have expanded either list, except by collecting the gecko, *Hemidactylus mabouia*, which I presume is present, if unrecorded, on both.

My count of 46 is too low. An unnamed but well-vegetated island of more than a hectare lies off Key Point, south of the western peninsula of Peter Island. Most people assume it to be part of that island, but I am assured (Marler, personal communication) that it is disjunct. Two rocks south of Dead Man's Chest appear to have shrub-stage vegetation as viewed from the heights of Peter Island. A rock separated from the southwest tip of Norman Island requires investigation. A separated, southern chunk of the Carrot Rock scarp should be climbed. There may be more.

Within historic times (though no one

living seems sure just when) "Pelican Cay" (not Pelican Island) was amalgamated with Little Jost Van Dyke by a (now) well-vegetated tombolo of cobbles and sediment; it lost its status as an island. In temporal similarity (and uncertainty), however, Green Cay was fragmented in two; its erstwhile southern terminus is today fully disjunct and called Sandy Spit. That is one of the smaller land areas on earth with two species of native reptiles. Man's activities have connected Wickhams Cay and Nannie Cay to the Tortola mainland with solid fill; these are not given separate consideration. Frenchmans Cay was separated from Tortola historically by mangrove swamp. Fill was built up to make a causeway from Tortola almost to the cay, and a channel ca. 2 m wide was

dredged (and bridged); Frenchmans Cay has been considered here as a separate island.

An island measuring ca. 50 × 100 m, showing the symbol for scrub vegetation, is a prominent feature on Directorate of Overseas Surveys (1959) map of Anegada, labelled "Little Anegada." It is imaginary. The real Little Anegada is a tiny (ca. 3 × 5 m), wave-washed block of limestone, ca. 30 cm above water at mean low tide. It is vegetated only with the maritime plants *Susuvium portulacastrum* and *Rhizophora mangle* (one). "In before time," states Mr. Lance Vanterpool (personal communication), "it was no bigger, but it was more prominent because here were not all these mangrove groves." The more recent map, Directorate of Overseas Surveys (1977) quite correctly shows the region as mangrove continuous with Anegada itself. The place where the imaginary "Little Anegada" was located in 1959, is, quite correctly, open water.

Much herpetological work had been done in these islands before I arrived. Lists were available, prepared by Maclean *et al.* (1977) from Schwartz and Thomas (1975) and Philibosian and Yntema (1976, 1977, 1978). Heatwole (1976) had examined *Anolis cristatellus wileyae* from eight additional islands. Nevertheless, there were no data for 18 islands. I obtained 13 new records for 10 islands with extant lists, and 44 new records altogether. Nevertheless, I must have failed to find many populations, and there is undoubted necessity for far more work.

I missed populations for three major reasons: 1) I had to average over a cay per day in my field inventory; this is obviously far too little time for even the tiniest land areas. 2) I was on the ground at the height of the dry season in an unusually arid year; many species were cryptic, especially by midday, and some may have been in brumation. 3) I am me. I have poor vision and a gimp leg, and some say I move more slowly than I did a quarter-

of-a-century ago—and climb less high. And, I do not like to hunt frogs too small to eat (all in these islands are that). However, from a theoretical point of view, the fact that I missed lots of populations will, I hope to demonstrate, prove trivial.

THE FAUNA

Maclean *et al.* (1977) list 23 species of reptiles and amphibians occurring in the British Virgin Islands. Of these, at least one, *Anolis cuvieri*, is not known from specimens; Schwartz and Thomas (1975) note that its existence on Tortola has remained "unverified for over a century." Perhaps it should be deleted, but I saw fine habitat for this species in the big ghuts draining Mount Sage, on Tortola, and on the rugged eastern slopes of adjacent Beef Island. *Anolis cuvieri* could occur here.

Another species, the tortoise *Geochelone carbonaria*, is a suspected introduction. It is today unknown from Peter Island, whence listed, and rarely seen on Tortola. It is reported to occur on Virgin Gorda. Tortoises of one sort or another were widespread in the pre-Columbian Antilles (Auffenberg, 1967, 1974); no one has done the sort of study of geographic variation in *G. carbonaria* needed to demonstrate its true status, spurious or otherwise. I leave it in.

I have previously (Lazell, 1973) discussed the notion that *Iguana iguana* was introduced to these islands, the northern limit of its range. The *I. iguana* seen and collected during the present investigation support my earlier view: they are native.

On three rock cays, where I believe reptiles probably occur, I failed to obtain specimens: Carval, North Cockroach, and the Indians. All support sea grape (*Coccoloba uvifera*) clumps and other vegetation. I believe *Anolis* (probably *A. cristatellus wileyae*) live on them, but weather conditions prevented me finding the animals on North Cockroach. I was

unable to climb to the best vegetation on Carval and the Indians.

Mirecki (1977) led a group of four ornithologists and a botanist to the islands in 1976. I visited all the islands they failed to, and 11 more they did not consider. However, Dr. J. D. H. Smith (personal communication) even went onto rocks with a few sedges where he reports seeing no lizards.

The results of all this are presented in Table 1, where the islands are ranked in order according to area. Despite the numerous new island records, the fauna presented no surprises whatsoever until 4 April, 1980, when I climbed the sheer face on the northeast side, tunnelled through the *Coccoloba*, and entered the strange world of Carrot Rock. Apart from the previous three weeks, I had been out of *Anolis* work in the Antilles for over a decade, but I there saw my next new one:

*Anolis ernestwilliamsi*¹ sp. nov.

Figures 2, 3

Holotype. MCZ 158395, an adult male, J. Lazell coll. 4 April, 1980.

Type locality. Carrot Rock, south of Peter Island, British Virgin Islands, 18°19'45" N, 64°34'18" W, Caribbean Sea.

Diagnosis. An alpha section *Anolis* of the *crstatellus* group *sensu* Williams (1976:17), attaining very large size (to at least 82 mm SVL), combining the following two scale characters: 1) scales small, 34 to 45 (av. 40) middorsals contained in the standard distance at midbody; 2) digital pads large, males with 24 to 27 lamellae, females with 20 to 22 lamellae, under the second and third phalanges of the fourth toe; and combining the following three color characters: 1) chin tricolored, with a bold, reticulate or barred pattern of near-black to grey on lighter blue-grey,

with egg-shell white to creamy blotches. In the male the dark chin elements extend onto the anterior throat fan; in the female they extend posterior to at least the level of the eye. 2) Latero-dorsal trunk and neck boldly patterned with near-white to yellow spots and marblings, coalescing to form stripes, and isolating spots of darker pigment ventrolaterally. 3) A dark bar or blotch on each side of the sacrum, set off posteriorly by a pale, ashy or tan border. In the females the middorsal stripe is irregularly edged, often fragmented, and in poor contrast to the bold latero-dorsal pattern.

Description of the type. MCZ 158395 is an adult male 81 mm SVL, with a standard distance 13.8 mm. There are 42 middorsals, 33 ventrals, and 53 dorsals (eight rows lateral to the middorsal line) contained in the standard distance at midbody. There are 26 lamellae under phalanges II and III of the fourth toe. There is an enlarged, double row of bluntly tectiform middorsals. The ventrals are smooth posteriorly and become tectiform to keeled anteriorly (chest region). There are seven loreal rows (left side); seven scales border the interparietal; there are seven plates across the snout between second canthals; there are 22 mental rows between third infra-labials.

In life the type was somber, dark grey-brown with olive tints on the limbs, tail, and lateral body. Near-white to cream-yellow spots coalesced to form streaks and marbling which became especially bold ventrolaterally. Slaty to sooty blotches and bars were scattered over the dorsal surfaces and were boldly set off on the ashy venter. There were yellow tones ventrally on the limbs and abdomen. The throat fan was deep crimson with a dark green center and scales that could change from white to grey. The anterior 30° of the extended throat fan was boldly reticulated with slate- and blue-grey with cream white. This tricolored pattern covers the entire chin region back to the jowls.

¹This name commemorates the man who, in 1958, agreed to pay my way back to Dominica if I could prove that island was occupied by one, not four, species of *Anolis*.

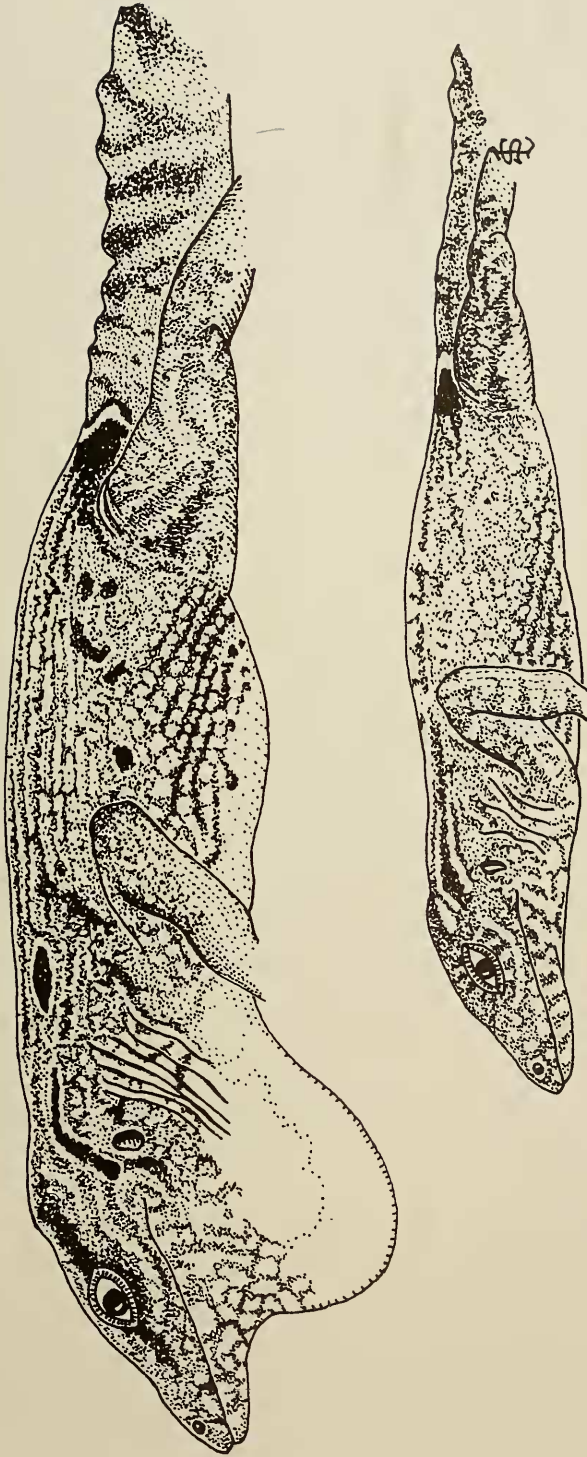


Figure 2. *Anolis ernestwilliamsi* sp. nov., from Carrot Rock, British Virgin Islands. The type, MCZ 158395, above; an adult female paratype, MCZ 158402, below.

17 Little Jost Van Dyke	63	120	3	H	X	X	X			
18 Mosquito	50	95	5	O	O	O	O			O
19 Great Dog	33	89	3	X	X	X	X			O
20 Necker	30	32	5	O	O	O	O			
21 Frenchmans	24	131	3	X	X	X	X			
22 Little Thatch	24	100	3	X	X	X	X		X	
23 Little Tobago	22	92	2	X	X	X	X			
24 Buck	17	56	3	X	O	S	S			
25 Little Cananoe	16	31	3	H	X	O	O			
26 George Dog	15	82	3	H	X	S	S			
27 Dead Mans Chest	14	66	3	O	X	O	O			
28 West Dog	13	49	1	X						
29 Fallen Jerusalem	12	46	4	O	O	O	O		O	
30 Eustatia	11	52	3	H	X	X	X			
31 Round Rock	7.6	62	4	O	O	O	O		O	
32 Green Cay	6.7	35	2	O	O	O	O			
33 Sandy Cay	5.5	22	4	O	O	O	O		O	
34 Pelican	3.4	59	2	X	X	X	X			
35 West Seal Dog	1.9	33	1	H						
36 Carrot Rock	1.3	28	1							X
37 Marina Cay	1.0	4.8	5	X	S	O	X			X
38 Broken Jerusalem	0.9	9.8	1	X						
39 Carval	0.8	36								
40 East Seal Dog	0.8	24	1	H						
41 Bellamy Cay	0.7	3.0	2	X	X					
42 South Cockroach	0.4	21	1	X						
43 Indians	0.2	21								
44 Saba Rock	0.2	4.8	2	O	X					
45 North Cockroach	0.1	16								
46 Sandy Spit	0.1	1.0	2	H	X					

● = species listed by Maclean, *et al.* (1977) and confirmed by me.○ = species listed by Maclean, *et al.* (1977), but not seen by me.H = *Anolis c. wileyae* listed by Heatwole (1976) and confirmed by me.

X = collected by me.

S = seen by me but not collected.

? = questionable occurrence.

The sacro-iliac region was pigmented on each side in a rough triangle of sooty color, set off posteriorly by ashy-white.

Variation. Ten paratypes, six males and four females, were collected by me and George Marler on Carrot Rock, 18 April, 1980. The males are MCZ 158396-8 and 158400-1; the females 158402-4. A male, MCZ 158399, and a female, MCZ 158405, have been deposited in the British Museum (BMNH 1980.1-2).

The largest adult male, MCZ 158396, was 82 mm SVL, fresh. The smallest, judged adult in the field on the basis of territorial defense, courtship, and display, was MCZ 158399: 71 mm SVL. Two juvenile males, MCZ 158400-1, measure 63 and 59 mm SVL, respectively. Females measure 52 to 60 mm SVL; MCZ 158402 is the largest. Two 52 mm females are apparently immature. One, MCZ 158404, shows some beginnings of ovarian activity on both sides, with larger yolks present on the right, but seems

never to have laid an egg. The other, MCZ 158405, is definitely immature. A 57 mm female, MCZ 158403, has a well-developed ovarian egg on the left and an apparently recently spent oviduct on the right; she was mature.

The standard distance varied from 17.0 to 18.3 (av. 17.4) percent of SVL in males, and from 17.2 to 19.0 (av. 18.0) in females. The difference is not significant with the small sample sizes available. Except for lamellae and ventrals, discussed below, meristics were combined for both sexes.

Dorsals counted in the standard distance at midbody eight rows lateral to the midline varied from 45 to 53 (av. 49). Mid-dorsals in the same distance varied from 34 to 45 (av. 40). There were 6 to 8 (av. 7) loreal rows, 5 to 7 (av. 6) postrostrals, 20 to 28 (av. 25) scales between third infralabials, 8 to 11 (av. 10) suboculars, 5 to 8 (av. 7) scales across the snout between second canthals, and 12 to 18 (av. 15) circumparietals. I do not know how Heatwole (1976) quantified forearm scales, but I can see no obvious difference between the new species and *A. cristatellus* in this regard, so have omitted the character.

Sexual dimorphism in lamellae count is striking. Males have 24 to 27 (av. 26), females 20 to 22 (av. 21). There is also strong dimorphism in ventral scale size, quantified as midventrals in the standard distance at midbody. Males have 28 to 34 (av. 31), females 23 to 27 (av. 25). All specimens are plotted for these counts in Figure 4.

There is variation in the placement of the spots, streaks, mottlings, and marblings on the dorsal and ventro-lateral surfaces. However, these are always bold and prominent. Color change is from darker to lighter, and often enhances the markings in the disturbed extreme. There is real variation from a browner extreme (MCZ 158396) to a greyer extreme (MCZ 158399). The light pattern elements may approach white (MCZ 158400) or be quite bright yellow (MCZ

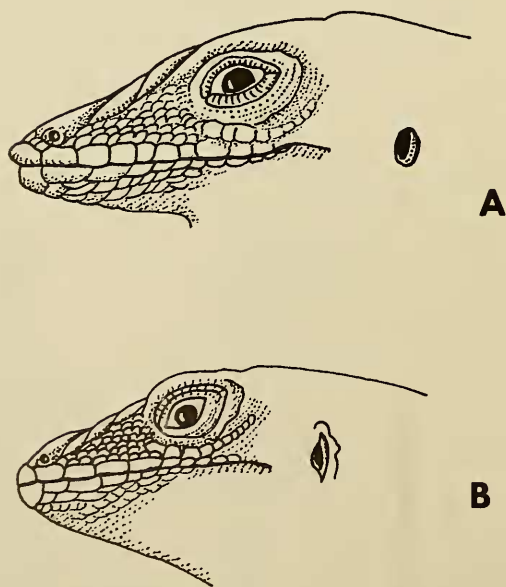


Figure 3. Head shape in two *Anolis*. A. *A. ernestwilliamsi* sp. nov., type-specimen, MCZ 158395, from Carrot Rock. B. *A. cristatellus wileyae*, type-specimen, MCZ 34792, from Culebra.

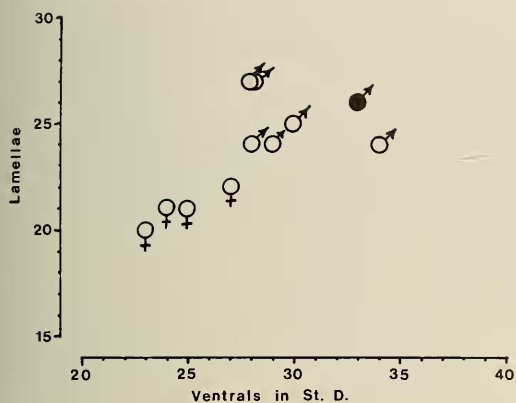


Figure 4. Sexual dimorphism in *Anolis ernestwilliamsi* sp. nov. from Carrot Rock. ♂ = type-specimen. See text.

158397). In both males and females the throat fan is deep crimson with a green center and white to grey scales. The female fan is quite small. The large male fan is variably invaded by the tricolor chin pattern elements anteriorly. In MCZ 158397, only about 20° of the extended fan is grey, blue, and cream. In MCZ 158396 nearly 40° of the fan is so patterned.

The sooty sacral blotch is prominent on all specimens, varying slightly in size and considerably in shape. The irregular, ashy middorsal stripe fades with age. The two smallest males retain it. Probably females retain portions of it throughout life, but in the large female (MCZ 158402) it was fading to obsolescence.

Comparisons. Heatwole (1976) provides an exhaustive account of geographic variation in *Anolis* of the *cratatellus* group on the Puerto Rico Bank and its satellites. He did not separate the sexes even with respect to lamellae count, and I do not find sexual dimorphism as pronounced in *A. cratatellus*—even *A. c. wileyae*—as in *ernestwilliamsi*. I counted 30 female *wileyae* and got 16 to 19 lamellae (av. 17); no overlap with female *ernestwilliamsi*. In males overlap occurs only in the Ramos,

Isleta Marina, and Villa del Mar populations where there may be 25, 24, or 25 lamellae, respectively. Two of these Puerto Rican coastal cays, Ramos and Isleta Marina, are populated by *A. c. cratatellus* × *wileyae* intergrades which cannot look much like *A. ernestwilliamsi*. At both Isleta Marina and Villa del Mar the scales are much larger than in *A. ernestwilliamsi*.

Anolis cratatellus has a shorter snout, on the average, than does *A. ernestwilliamsi*; in males it is 15.3 to 17.8% SVL (av. 17.0) and in females 16.4 to 18.2 (av. 17.2). Once again, the difference between sexes is insignificant, but the difference between species is significant at the 95% level of confidence. This difference does bias counts higher for *A. ernestwilliamsi* whenever the standard distance is used, but the scale size difference is real nonetheless, as can be seen from comparing like-sized individuals (e.g., MCZ Z-08348: *A. c. wileyae*; MCZ 158399: *ernestwilliamsi*).

Heatwole (1976:10) comments on the cline in scale size seen in *A. c. wileyae*: as one proceeds eastward from Puerto Rico through the Virgins, the anoles have lower counts—therefore larger scales. *A. ernestwilliamsi*, residing about 76% of the way along that cline, stands in bold contrast to it, with the smallest scales seen in any member of the complex.

I am not enamored of size as a taxonomic character in reptiles. Nevertheless I am compelled to admit the importance of size in the relationships of *A. ernestwilliamsi*. I measured 135 females of *A. c. wileyae*, and the largest I can find are 50 mm SVL (MCZ Z-08400, George Dog; MCZ 60635, Palominos, E of Puerto Rico; and MCZ 127725, Seal Dog). Some females of *A. c. wileyae* are producing eggs at 32 mm SVL: MCZ 35734, Vieques. Females of *A. ernestwilliamsi* from Carrot Rock may still be immature at 52 mm SVL (see above). Thus there is no evidence of overlap of sizes of mature females.

There is some overlap in sizes of males

that seem mature. Thus, large males of *A. c. wileyae*, MCZ Z-08348, from Broken Jerusalem, and MCZ 128484, from Culebra, are both 72 mm SVL, just larger than MCZ 158399, the smallest mature *ernestwilliamsi*. One male *wileyae*, MCZ Z-08429, from South Cockroach is a giant for his kind, measuring 75 mm SVL; he has 31 middorsals and 23 lamellae. MCZ Z-08429 has the shortest snout measured, 15.3% SVL, and was nearly patternless brown in life. None of the large *wileyae* approaches the color characters of *ernestwilliamsi*; none has more than 33 middorsals in the standard distance or 23 lamellae.

The three color characteristics which taken together are diagnostic of *ernestwilliamsi* can all be seen singly or weakly developed in occasional specimens of *A. c. wileyae*. MCZ 138543 (Estate Tutu, St. Thomas) combines a bold chin pattern with sacral marking like that of *ernestwilliamsi*; however, it lacks the dorsal and latero-ventral pattern. Conversely, MCZ Z-08409 (Eustatia) has fine trunk pattern but lacks the tricolored chin and sacral blotch. An adult male from Beef Island, MCZ Z-08436, was less boldly marked but a close approach to the color characters of *ernestwilliamsi* in life. The chin pattern was bicolor—dark grey and pale blue-grey—however, and there are only 33 middorsals and 22 lamellae. The closest approach to *ernestwilliamsi* I can find is MCZ 35952, from Culebra. This specimen is faded and may not have had a tricolor chin. Nevertheless, the pattern elements that remain closely resemble those of *ernestwilliamsi* in all three respects. The specimen just overlaps *ernestwilliamsi* in middorsal count with 34, but has only 23 lamellae. It is a seemingly adult male, but very small: 48 mm SVL.

There is a strong distinction in head shape of *A. ernestwilliamsi* relative to all *A. cristatellus*, but difficult to quantify. Basically the head of the Carrot Rock species is longer, lower in profile, the rostral bulge is longer, lower, and more gently tapered, and the angle the rostral

makes with the mouth is oblique, not rectilinear. These differences are shown in Figure 3.

In summary, *Anolis ernestwilliamsi* is closely allied to *Anolis cristatellus* and shares its presacral vertebral count of 23, as do *monensis*, *desechensis*, and *scriptus*. *A. ernestwilliamsi* differs from all of these, and from Puerto Rican *A. c. cristatellus* in throat fan color, just as does *A. c. wileyae*. From this last form, its closest neighbor, *A. ernestwilliamsi* is distinct in combination of color characters, small scales, high lamellae counts, large size, and head shape. For those of us who like quick, quantitative ways to separate species, *A. ernestwilliamsi* may be separated from *A. cristatellus* by simply dividing the lamellae count into one hundred minus the middorsal count. In Figure 5 I have plotted this against snout-vent length to graphically portray the distinction.

Habitat and behavior. Carrot Rock is steep-to and cliffed for virtually all of its perimeter. The vegetated top of the ca. 1.2 ha islet is a canted plateau rising from ca. 6 m above sea level on the windward side to 27.6 m on the lee. The surface is a deceptively uneven boulder field.

The deception is perpetrated by the vegetation, which covers the surface rather evenly. The dominants are the polygonaceous sea grape, *Coccoloba uvifera*, and leguminous vines. Main stems of these plants may reach 30 cm and 5 cm, respectively. The plants grow prostrate and sprawling over high points on the boulder substrate and canopy pockets or low areas rather like caclin bush (*Clusia mangle*) does in the high Lesser Antilles (Lazell, 1972). There are small areas with soil in which grow grasses and sedges, especially near the crest of the cay.

The anoles live primarily on the rocks (to a lesser extent on the vegetation, especially sea grape trunks) under the canopy. This is a shady, dimly lit zone, cooler and somewhat protected from the full force of the tradewinds.

Anolis ernestwilliamsi is quite com-

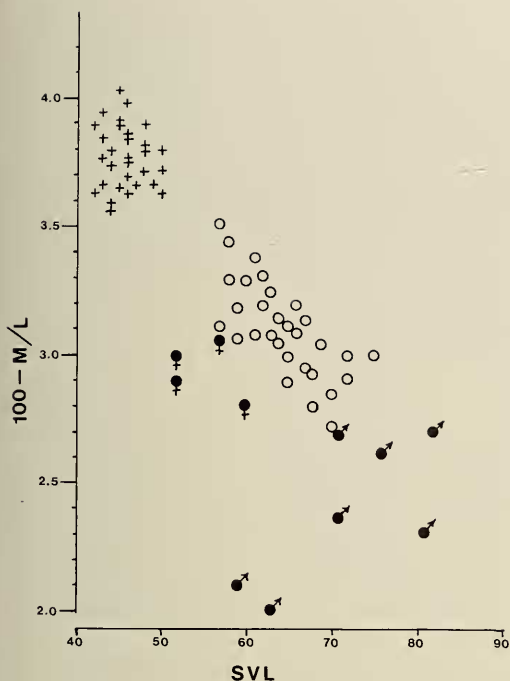


Figure 5. A graphic depiction of the morphometric distinction between *Anolis ernestwilliamsi* sp. nov. (solid symbols), and *A. cristatellus wileyae* (males, O; females +). M = middorsals counted in the standard distance. L = subdigital lamellae.

mon in its habitat. Sitting quietly in a pocket below the vegetation, I could count two to four in ca. 100 m². I estimate about two-thirds of the island provides good habitat, so a population of two to three thousand individuals is not unreasonable.

My observations indicate a balanced sex ratio. Both sexes bob and fan in the manner of the widespread *A. c. wileyae*. Apparently sexual maturity is attained at sizes larger than 63 mm SVL in males and 52 mm SVL in females. The largest female, MCZ 08460, 60 mm SVL, has a large egg in the left oviduct and a smaller one in the right. This implies the alternating oviduct, single egg laying strategy common in Antillean anoles (Lazell, 1972). The 57 mm female (MCZ 158403) was yolking up a large egg on the right

and seemed to have just laid an egg from the left at time of capture.

Small islands in the British Virgins (like those elsewhere in the Antilles) are occasionally burned over and frequently used for raising such livestock as goats. No evidence of fire or goats was visible on Carrot Rock, and its difficulty of access may eliminate the temptation to so abuse it. While I have no evidence that either burning or goat browsing extirpates lizards, I would certainly regard either or both with grave trepidation on Carrot Rock. In view of Carrot Rock's remarkable nesting seabirds (Lazell *et al.*, 1982)—none of which utilize the vegetated upland—and *Anolis ernestwilliamsi*, this islet should be set aside as a sanctuary or preserve. Limited collecting of the anole, especially by the technique of noosing individuals around the edge of the vegetated top, can do no serious harm, but such collecting should be regulated (see Lazell, 1980a).

Discussion. Heatwole's (1976) taxonomic conclusions are difficult for me to understand. It is unclear to me why the karyotypic difference between *A. monensis* and *A. cristatellus* augurs for the species status of *A. desechensis* (Heatwole, 1976:13). In any case, karyotypic differences are not always indicative of species status in *Anolis* (or other vertebrates): Hall (1974). All the scale counts provided for *desechensis* are included within the range of variation of Puerto Rican *cristatellus*, leaving no device for separating *desechensis* from the yellow-fanned form in southwestern Puerto Rico. Scale characters are not specified (on p. 7 Heatwole alludes to a difference in postrostrals but his Figure 4 belies it), and probably only modal.

I agree with Heatwole (1976:12-13) that *A. c. wileyae* is an indivisible entity. The statistically significant differences Heatwole found fall far short of taxonomic significance. I find it impossible to frame diagnoses that would separate 75% of Vieques specimens, for example, from those in the Anegada population—at the opposite extreme of the range. (I have

examined 21 Anegada specimens: U.S. National Museum of Natural History 140309-10; MCZ 12145-56 and 35704-10.)

Against this background it is easy to defend *Anolis ernestwilliamsi* as a full species. Even granting that the minor karyotypic difference between *crisatellus* and *monensis* bequeaths species status to them, and assuming that *ernestwilliamsi* has the *crisatellus*-like complement of 27 (as one suspects *desechensis* does), *ernestwilliamsi* is far more different from any of these previously named forms than they are from each other. It does not fit into the pattern of geographic variation shown by the intergrading forms of *Anolis crisatellus*, and geographically proximate populations of *A. c. wileyae* show no hint of character approach.

I fought my way through dense scrub on Peter Island to reach Stoney Bay, the southern edge of which is the closest land to Carrot Rock, and there collected a series of typical *A. c. wileyae* (MCZ 158927-31). This most proximate habitat is a xeric woodland dominated by gumbo-limbo (*Bursera simarouba*), figs (*Ficus* sp.), and mangroves (*Rhizophora mangle* and *Avicennia rhizophorarum*). A bay head barrier of cobbles, coral, and slabs that look like limestone fronts the sea. Anoles were scarce, but there were geckos (*Sphaerodactylus macrolepis*), iguanas (*I. iguana*), skinks (*Mabuya sloanei*), and kestrels (*Falco sparverius*). Standing on the cobbles I could identify to species the tropic birds (*Phaethon aethureus*) wheeling over their nest sites on Carrot Rock, a scant 450 m away. I wondered if the tropic birds ever alighted over here, or the kestrels over there. So far as I know, I am the only living thing which has ever been both places.

Anolis ernestwilliamsi is an autochthonous endemic on its peculiar little cay. It must have evolved very rapidly (see Lazell, 1972: 102-103) in a few thousand years of isolation.

Electrophoretic, karyotypic, and ethological studies of *Anolis ernestwilliamsi* are certainly called for. On present evidence, its status as a full species seems to me more secure than that of *monensis* or *desechensis*. Granting that tastes differ on these points, dialogue and exposition will prove useful to those of us particularly interested in insular speciation and geographic variation.

OTHER FORMS

I suggest some nomenclatural changes not commonly in use today. Previously (Lazell, 1973) I commented on the trivial nature of the putative distinctions between "*Cyclura*," "*Brachylophus*," and *Iguana*. Examination of specimens reveals that even these differences are modal; I refer to all species in the complex as *Iguana*.

Maglio (1970) regarded the Caribbean colubrids as "oversplit." I concur. The entire complex of "*Alsophis*," "*Dromicus*," "*Arrhyton*," and *Liophis* are closely comparable to *Anolis* or *Eleutherodactylus* (or *Iguana sensu lato*) in diversity. Differences in dentition, cranial bone proportions, coloration, and hemipenes are, I suggest, reflections of character divergence among very closely allied species. Certainly the two Virgin Island species are congeneric; they seem a near perfect analog of the sympatric lizard pair *Anolis crisatellus* and *A. pulchellus*. The oldest name for this assemblage of snakes seems to be *Liophis*; it is used herein.

The species and their distributions are tabulated (Table 1). I have previously (Lazell, 1980a) listed four origins for members of this herpetofauna: 1) Species widely distributed on the greater Puerto Rico Bank stranded today in the Virgins by post-Wurm sea level rise. 2) Species coming from the west (Greater Antilles and other Puerto Rico Bank islands) across water. 3) Species coming from the east and south (Lesser Antilles) across water. 4) Autochthonous endemics

whose original ancestors may have come by any of the first three methods.

I cannot envision a way to separate examples of the first and second categories. I suspect most of the herpetofauna belongs to the first category, but it is truly unfortunate that I cannot perceive examples of the second, for they would be most interesting.

Four species (ca. 17%) came by the third method from the Lesser Antilles: *Hemidactylus mabouia*, *Thecadactylus rapicaudus*, *Iguana iguana*, and *Geochelone carbonaria*.

Five species (ca. 25%) are endemic to the islands east of Puerto Rico at full species level and are not known to have ever occurred on Puerto Rico: *Amphisbaena fenestrata*, *Sphaerodactylus parthenopion*, *Iguana pinguis* (?), *Anolis ernestwilliamsi*, and *Eleutherodactylus schwartzi*. There are bones of an *Iguana* near *pinguis* from Puerto Rico. Of these forms the last four are today known only from the British Virgin Islands (Lazell, 1980a). All of these species seem most likely to have been derived from Greater Antillean (in fact Puerto Rican) stocks. If one assumes that speciation began after the retreat of the Wurm, the processes have been rapid indeed. This is not, of course, necessarily the case, but seems most likely for at least *Anolis ernestwilliamsi*.

THEORIES OF BIOGEOGRAPHY

Two disparate and sharply contrasting theories of island biogeography have emerged in recent years. The first, published by MacArthur and Wilson (1967), is essentially abiological. It attempts to explain faunas (or floras) entirely in terms of measurable physical and/or temporal parameters such as island area, elevation, distance from a source of propagules, or length of time of island separation. The implicit philosophical basis of this theory is that biological phenomena and situations, like those in chemistry and

physics, should be reducible to symbols and numbers, which, in turn, can be arranged in mathematical formulae that "predict" (or postdict) similar biological phenomena or situations.

A necessary adjunct to the MacArthur and Wilson view is that time of island separation cannot matter very much because a large fauna stranded by rising sea level must necessarily dwindle by extinctions to the "right" number of species for an island with similar physical parameters which was never part of a larger land area. This notion has been hotly debated (see Simberloff, 1976, and works cited therein).

It is interesting that the MacArthur and Wilson theory germinated from Darlington's (1957) little rule of thumb which stated that Antillean herpetofaunas increase by *roughly* a factor of two for every increase in island size of a factor of ten. MacArthur and Wilson explicitly believed that, by measuring other parameters and coalescing them into ever more complex formulae, the roughness in Darlington's rule could be eliminated: the biota of an island should be calculated with little more difficulty than Boyle calculated pressure, given volume and temperature.

Lack's (1976) view of islands is considerably more complicated. While he did not doubt the importance in a general way of obvious physical features like island size, he was deeply impressed by biotic factors as well. He was impressed by the fact that, cumbersome as the formulae became, they still failed to "predict" (or, correctly, postdict to the time the data were collected) the right numbers in many cases. Most importantly, however, Lack was impressed by the resilience of insular faunas: apart from the artificial and edificarian catastrophes wrought by man, and often in spite of them, the predicted extinction rates were simply way out of line with apparent reality. Far from becoming extinct or replaced by new colonizers, insular populations often tended to expand their

niches and resist propagule input for so long that evolution carried them to the far realms of the bizarre. The dodo, Lack might have said, was just a pigeon which lived alone too long—but very, very long indeed. Many recent data on population genetics within the well-studied species *Felis catus* support this view of impenetrable matrices: Blumenberg (1977); Todd and Blumenberg (1978).

Lack's view may have grown from his field work in the Galapagos. Insular fragmentation may not result in diminished faunas at all. Quite the contrary, it may well lead to spectacular radiations.

The number of forms of finches, or tortoises, or lizards increases (very roughly) as a function of the number of islands. Since rising sea level increases the number of islands, the fact that it decreases their size may utterly fail to reverse the trend of species proliferation. *Anolis ernestwilliamsi*, possibly *Iguana pinguis*, and the subspecies of *Typhlops richardi* and *Liophis portoricensis* are examples of this trend in the British Virgins.

ANALYSIS

When a person has a poor ear for music he will flat and sharp right along without knowing it. He keeps near the tune, but it is *not* the tune.

—Mark Twain, 1895

Of the 43 islands with presently demonstrated herpetofaunas, only two—Great Tobago (two species; 88.6 ha) and West Dog (one species; 12.5 ha) fit the area-species curve of MacArthur and Wilson (1967:Fig. 2). All the rest have “too many” species. Tortola, Virgin Gorda, and Peter Island, for example, all have about three times the predicted number. Extrapolating the MacArthur and Wilson curve indicates that islands of less than ten hectares should have no species at all. More than 30% of the British Virgin Islands diverge from MacArthur and Wilson's predictions,

therefore, by an infinite factor. The relationship of area to number of species is shown in Figure 6.

Using the basic formula of MacArthur and Wilson (1967:8), but with new numbers, we find:

$$S = 1.63 A^{0.233}$$

Spearman $r = 0.797$, $p = 0.01$, which is reasonable: larger islands do tend to have more species. Extrapolating this curve into the realm of no species present indicates that at least one species should be present on any island of ca. 50 m² or greater. While this prediction will be most interesting to test, it is certainly less unreasonable than the previous 10 ha prediction.

The value $Z = 0.233$ is far lower than MacArthur and Wilson cited for any other fauna except land and fresh-water birds in the West Indies (1967:9). As Z approaches zero, the importance of area diminishes (at $Z = 0$ the formula becomes $S = C$).

Using the new, “improved” formula, 14 islands (nearly a third: 32 percent) have “too many” species and 11 islands (more than a quarter: 26 percent) have “too few.” Therefore, 58% of the islands fail to fit even the new predictions. It is important to understand that a biogeographic formula with a positive correlation of 80% is still *wrong most of the time*.

The cases involving too few species are, I must admit, probably the result of collecting failure. Great Thatch, Scrub, Great Tobago, West Dog, and Pelican are all “missing” two species. Cooper, Little Jost Van Dyke, West Seal Dog, East Seal Dog, Carrot Rock, and Broken Jerusalem are all “missing” one species each. Of these only Carrot Rock was examined carefully by me. Nevertheless, I believe additional search at a wetter season will reveal at least one more species there, and I believe all these islands are good for more species than are known at present. Finding the “missing” species will

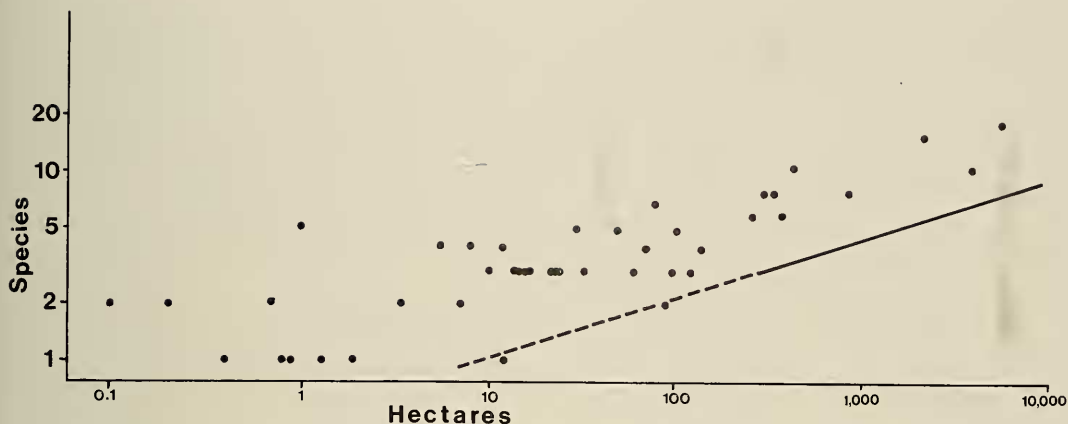


Figure 6. Area-species relationships. Dots represent the 43 British Virgin Islands with presently known herpetofaunas. The solid line is the curve shown by MacArthur and Wilson (1967: Fig. 2). The dashed line is the extrapolation of this curve to the point where no species would be predicted present by MacArthur and Wilson (1967).

have a profound effect on the formula and the next generation of predictions. The value of C will be elevated; therefore the predicted size for a minimal area island harboring one species will be even less than 50 m^2 . The value of Z will be reduced. Therefore the importance of area in the calculation will diminish.

Islands with too many species are far more embarrassing for advocates of a MacArthur and Wilson approach to biogeography. Of the islands with only one species "too many" the error is only about one-fifth for Mosquito and Necker (each with five species). On Fallen Jerusalem the error approaches 30% and on Round Rock it is more than a third (both have four species). For Saba Rock and Sandy Spit the failure of prediction is about 50%.

Of islands with two species "too many," Great Camanoe and Guana are not egregiously in error at about 20 to 25%. Sandy Cay (with four species) is about half off predicted, but Marina Cay (with five species on one hectare) is "wrong" by a factor of more than two-thirds.

The larger islands are little closer to

predicted values. All have counts 36 to 39% too high. This means that Salt Island has three species "too many," Peter has four, Virgin Gorda six, and Tortola has seven species more than predicted by the formula. Errors of this magnitude and frequency render the formulation useless to me as a practicing field biologist.

There is a weaker but "good" correlation of elevation (E) to species number: Spearman $r = 0.586$, $p = 0.01$. Using both kinds of data and searching for the best formulation in terms of least root mean square error (Smith, 1977: 257), one gleans:

$$S = C_1A + C_2E + C_3$$

Where:	$C_1 = 0.00198$	$C_2 = 0.016$
	$C_3 = 2.1$	RMS = 1.65.

This formula is strongly appealing mathematically because it represents a canted, but flat, plane rising in three dimensions. The fact that it rises from $A = 0$, $E = 0$, $S = 2$ —an island with neither area nor elevation, but with two (sodden) species—is a mathematically

inconsequential problem easily relegated to some lizard hunter for solution.

An interesting feature of this formula is that it values area less by an order of magnitude than it does elevation. This reverses the order of correlation produced when each factor was independently compared to species number *via* Spearman rank coefficients.

For islands > 100 ha the percent error for this formula is > 30 for only two islands: Peter (ca. 47% or five species "too many") and Great Thatch (78% or two species "too few"). Virgin Gorda has ca. 19 percent, or three species "too many." Of the twelve largest islands, the remainder are either off by one or two species (seven) and low percentages (10 to 30%) or are right on: two, Beef and Ginger Islands. In my opinion, both Beef and Ginger are undercollected and will prove to support several additional species in each case.

Of the 18 medium-sized (> 10, < 100 ha) islands, 13 have numbers of species differing from the prediction. The worst is West Dog, ca. 200% off with two species "too few." Great Tobago is more than 100% off also, and "missing" two species. Necker Island is more than 40% off with two species "too many," and Scrub errs about the same extent with two "too few." Salt Island is about 40% "wrong," with three species "too many." Buck, Little Camanoe, George Dog, Dead Mans Chest, and Eustatia are right on. The rest (eight) are off by one species; this amounts to an error of more than a third for Little Jost Van Dyke and Frenchmans Cay (both "too few"). For the remainder the percentage error is lower.

Of the 13 small islands (< 10 ha), ten have numbers of species differing from the prediction. Five of these have errors between 100 and 200%; of course the number of species "wrong" is usually just one, but both Carrot Rock and West Seal Dog are "missing" two species. Sandy Cay has two species "too many" and Marina Cay is the champion with

three species "too many." Bellamy Cay, Saba Rock, and Sandy Spit are right on.

Thus, using the new formula we get a much tighter fit in terms of percentage error in the larger islands (especially), but for 33 of the 43 islands—*more than three-quarters*—the formula is still *wrong*. As before, errors of "too few" will predictably be corrected by better hunting.

In attempting to find a fit that avoided the problem of $A = 0$, $E = 0$, $S = 2$ we fed the computer data for Carval, Indians, and North Cockroach, which have fine areas and elevations, but no known species. We also fed it the open ocean at $A = 0$, $E = 0$, $S = 0$. The computer could deal with this in the linear equation, but it did not help. It increased RMS but did not bring $C_3 = S$ below two significant figures. In exponential arrangements the log of zero cannot compute, of course. Giving tiny, false values permitted computation, but no exponential arrangement, with or without the $S = 0$ data points, was as good as the linear one.

A slight further refinement can be made to this formula utilizing the fact that there is some relationship between area and elevation (i.e., big islands tend to be higher than small islands):

$$S = C_1A + C_2E + C_3AE + C_4$$

Where $C_1 = 0.0025$ $C_2 = 0.019$

$$C_3 = -1.97 \times 10^{-6} \quad C_4 = 1.8$$

$$\text{RMS} = 1.60$$

The effect of the admittedly tiny, negative value of C_3 is to dip the plain for large areas and high elevations. The biggest and smallest islands are now right on. Discounting islands with "too few" species as examples of collector failure, however, there are still 13 islands—ca. 30%—with "too many." Peter Island is the worst by a factor of nearly 50% and five species. Virgin Gorda, Salt, Necker, and Marina Cay all have an excess of three species. Great Camanoe and Sandy Cay are off by two. Norman, Prickly Pear,

Mosquito, Little Camanoë, Fallen Jerusalem, and Round Rock are all overstocked by one species.

The computer still asks us to believe that the open ocean has two species (at $A = 0$, $E = 0$, $C_4 = 1.8$, which is two). Perhaps it wants us to acknowledge the existence of marine turtles. In all the formula provides the wrong answer for 31 of 43 islands, or 72%.

Increasing the number of points to 47 by feeding in the three $S = 0$ islets and the open ocean brought C_4 to one—which is only half as insane, one might say—but increased RMS to 1.63. There was no improvement: the formula was still wrong for three-quarters of the islands.

CONCLUSIONS

Statistics is a game played by computers which are just as intelligent as bowling balls. My acquaintance is not large, but I have yet to meet a computer which knew that 16 (the number of known species on Virgin Gorda) is not at all the same thing as 16.00000. I believe that if mathematically inclined biogeographers would be more sanguine about “good” correlations and actually calculate the percentage error between the observed species numbers and their formulas’ “predictions” (and pay attention to which percentage errors amount to species numbers) they would take a far less enthusiastic view of computer time and costs. As I have pointed out before (Lazell, 1976, 1979), to determine the number of species on an island one must at the very least go to the island and count.

One striking fact was available to MacArthur and Wilson (1967) before they published: I had already shown that Sombbrero—anchor point in Darlington’s (1957) table from which MacArthur and Wilson selected their data (1967: Fig. 2)—had three species present (Lazell, 1964). Most West Indian islands, in fact, have at least three species comprising a

herpetofauna standardly involving a member of the genus *Anolis*, a member of the family Gekkonidae, and some other form.

The Rule of Three in the Virgin Islands holds for 22 islands over three orders of magnitude in area: Table 2. All of these islands support *Anolis c. wileyae*. All but three (the American islands of Leduck Cay, Flanagan, and Salt Cay)—86%—also support the gecko *Sphaerodactylus m. macrolepis*. The teiid lizard *Ameiva exsul* is present on 15, or 68%. Other species making up the complement of three include a second *Anolis* (*A. stratulus*): five for ca. 23%; a skink (*Mabuya sloanei*): two for nine percent; a snake (*Liophis portoricensis*): two for nine percent; and a second gecko (*Hemidactylus mabouia*): one for less than five percent.

The Rule of the Irreducible Anole states simply that any West Indian islet, cay, rock, or spit which supports more than herb-stage vegetation—i.e., bushes or shrubs—will also support a member of the genus *Anolis*. This is not to be confused with Marler’s (1980) Mexican bush rule, albeit not wholly dissimilar. In my work in the Lesser Antilles (Lazell, 1972) I found but one islet—Green Cay off Saba—that had bushes (two *Coccoloba uvifera*) but no *Anolis* I could find. I believe every case of an islet in the British Virgins where I failed to find *Anolis c. wileyae* (Carval, Indians, North Cockroach) is simply that: where I failed.

I predict that subsequent work in these islands will add at least seven cays to those fitting the Rule of the Irreducible Anole (the three I failed to find *Anolis* on plus four unnamed ones). I predict that many islands now thought to fit the Rule of Three will turn out to have additional species, and many where less than three are known today will move up to fill the ranks. In short, I believe the fauna will certainly prove to be richer than is now known.

No extinction or extirpation need take place in the British Virgin Islands if reasonable conservation measures are en-

TABLE 2. THREE SPECIES ISLANDS IN THE VIRGINS.

Island	<i>Anolis c. wileyae</i>	<i>Sph. m. macrolepis</i>	<i>Ameiva exsul</i>	Other species	Area (ha)
1 Rotto Cay, A	X	X	X		0.8
2 Steven Cay, A	X	X		<i>Anolis stratulus</i>	2.4
3 Henley Cay, A	X	X		<i>Hemidactylus mabouia</i>	5.3
4 Cas Cay, A	X	X	X		7.1
5 Leduck Cay, A	X		X	<i>Anolis stratulus</i>	7.3
6 Cockroach I., A	X	X		<i>Liophis portoricensis</i>	7.7
7 Congo Cay, A	X	X	X		10.3
8 Flanagan, A	X		X	<i>Anolis stratulus</i>	10.5
9 Eustatia	X	X	X		10.5
10 Dead Mans Chest	X	X	X		14.1
11 George Dog	X	X	X		15.4
12 Little Camanoe	X	X	X		16.2
13 Buck	X	X	X		17.0
14 Little Tobago	X	X		<i>Mabuya sloanei</i>	22.3
15 Little Thatch	X	X		<i>Anolis stratulus</i>	23.5
16 Frenchmans	X	X	X		24.1
17 Salt Cay, A	X		X	<i>Mabuya sloanei</i>	25.6
18 Great Dog	X	X	X		30.3
19 Little Jost Van Dyke	X	X	X		57.2
20 Scrub	X	X	X		88.6
21 Great Thatch	X			<i>Anolis stratulus</i>	112
22 Hans Lollik, A	X	X		<i>Liophis portoricensis</i>	128

A = American islands with data from Maclean *et al.* (1977).

acted. I have already listed a number of endangered, threatened, and/or declining species and outlined plans to conserve them (Lazell, 1980a). In every case the decline, threat, or endangerment is strictly artificial: the direct result of human activities. In no case is a possible extinction or extirpation the foreseeable result of any natural phenomenon. Even tiny, overwashed Sandy Spit appears likely to accrete sediment on growing coral about as rapidly as sea level rises. I expect it to retain its two species and—with better search—prove to fit the Rule of Three, at least.

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